American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2511 FEBRUARY 20, 1973

Zoogeographical Significance of the Ricefield Rat, *Rattus argentiventer*, on Celebes and New Guinea and the Identity of *Rattus pesticulus*

By Guy G. Musser[1]

ABSTRACT

In the present report I document the identity of *Rattus pesticulus*, a taxon named and described by Oldfield Thomas (1921) from one specimen obtained in northeastern Celebes, with the ricefield rat, *R. argentiventer*. The ricefield rat lives in grasslands and fields of rice and has a spotty geographic distribution that extends from the mainland of Southeast Asia to the Philippines and New Guinea. I also list and discuss the scientific names that apply to *R. argentiventer* and point out the zoogeographic significance of its occurrence on Celebes and New Guinea.

Rattus pesticulus is a taxon known only from northeastern Celebes and one whose identity and proper allocation has been in doubt since it was originally named and described by Oldfield Thomas in 1921. It is one of the many taxa that needs to be defined before the number of species of *Rattus* that occur on Celebes can be determined and their morphological and ecological limits understood—a prerequisite to understanding the zoogeographic affinities of these species. In the present report I document the identity of *R. pesticulus* with the ricefield rat, *R. argentiventer*, a species with a spotty geographic distribution that extends from the mainland of Southeast Asia to the Philippines and New Guinea.

[1] Archbold Associate Curator, Department of Mammalogy, the American Museum of Natural History.

The present paper is not a taxonomic revision of *Rattus argentiventer*. As part of my study of the murid fauna of the Indo-Malayan and Indo-Australian regions I have worked through collections of *Rattus* in museums and have tried to sort out specimens of *R. argentiventer*, not only to verify published records of its occurrence on Celebes and New Guinea, but to augment information on its geographic distribution elsewhere. At present I only summarize morphological and ecological characteristics of the species and record its known geographic distribution. With that introduction to *R. argentiventer*, I then document its association with *R. pesticulus*, verify its presence on Celebes and New Guinea, and discuss the zoogeographic implication of its occurrence in those two areas.

At this point the reader should know that Dr. David H. Johnson, formerly with the National Museum of Natural History, Smithsonian Institution had been working on a systematic revision of species in the *Rattus rattus* group and had discovered long before I did, and long before most of the persons cited in the next section did, that samples of *argentiventer* represented a distinct species and not a subspecies or ecological race of *R. rattus* as it has always been recorded in the literature. As far as I know, Dr. Johnson has not published results of his studies on *R. argentiventer*, nor did he study the samples from Celebes and New Guinea. He did, however, share his knowledge about *R. argentiventer* in Southeast Asia and the Philippines with Kyle R. Barbehenn, Joe T. Marshall, Jr., and Paul Ryan.

Unfortunately, I have not had the opportunity to discuss the systematics of *Rattus* with Dr. Johnson, or to benefit directly from his knowledge about geographic distribution and taxonomy of the genus. I independently had concluded that *argentiventer* was a distinct species by working over the collections of *Rattus* in the American Museum of Natural History. Subsequently, I met Barbehenn, Marshall, and Ryan and each told me of his research and related the information that had been given him by Dr. Johnson. I have benefitted greatly from my discussions with them, and they have sharpened my insight into taxonomy of *R. argentiventer*. Thus, in a roundabout way, Dr. Johnson has had a strong and positive influence on the contents of the present report. I am grateful to him for his scholarship and for the information that has filtered down to me by way of his colleagues.

Abbreviations and Methods

Specimens I examined are in collections of the following institutions:

AMNH, the American Museum of Natural History, New York
ASRCT, Applied Scientific Research Corporation of Thailand (Centre for Thai National Reference Collections), Bangkok
MB, British Museum (Natural History), London

EJ, Refers to specimens collected by E. Jacobsen in Sumatra that are in the Rijksmuseum van Natuurlijke Historie. As yet they have not been registered and incorporated into the main collection of that institution.
FTMB, Faculty of Tropical Medicine, Bangkok
MNHN, Museum National d'Histoire Naturelle, Paris
MZB, Museum Zoologicum Bogoriense, Bogor
NMS, National Museum (formerly Raffles Museum), Singapore
RMNH, Rijksmuseum van Natuurlijke Historie, Leiden (includes the large private collection of H. J. V. Sody)
SMRL, SEATO Medical Research Laboratory, Bangkok, Thailand
USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.
ZMA, Zoological Museum of the University of Amsterdam

All measurements are in millimeters. Cranial measurements were taken with dial calipers graduated to tenths of millimeters; their limits are defined elsewhere (Musser, 1970a). I measured the greatest length and breadth of each molar with the calipers under a dissecting microscope.

WHAT IS *RATTUS ARGENTIVENTER?*

Rattus argentiventer is a rat that occurs in Southeast Asia, the Greater and Lesser Sunda islands, Celebes, Philippines, and New Guinea. The taxon was originally described as a subspecies of *R. rattus*, and it has long been regarded in the literature as one of the three "ecological subspecies" of *R. rattus* that occur in the Indo-Malayan and Indo-Australian regions (Sody, 1930, 1941; Chasen, 1933, 1940; Ellerman, 1949; Harrison and Traub, 1950; Laurie and Hill, 1954; Hill, 1960). The other two are *R. rattus diardii*, the house rat, a species that lives in and around dwellings of humans, and *R. rattus jalorensis*, the Malaysian wood rat (sometimes called the field rat), an inhabitant of second-growth forests, mixed scrub and grassland, and plantations of rubber trees and oil palms. The three forms are ecologically and morphologically distinctive and have been recognized as such by persons who have worked with populations of each kind in the field, laboratory, and museum (see, for example, Van Heurn, 1931; Chasen, 1933; Harrison, 1951, 1957b, 1961b; Wood, 1969, 1971b).

John L. Harrison, who has worked with all three forms in Malaya, suggested in 1961 that *diardii* was the only one of the three that could actually be considered a subspecies of *R. rattus* and that the taxa *jalorensis* and *argentiventer* were actually valid and distinctive species rather than ecological subspecies of *R. rattus*. This conclusion about the specific status of *jalorensis* and *argentiventer* has been independently supported by other biologists (Dhaliwal, 1961, 1962, 1964; Medway, 1965, 1969; Van Peenen, Ryan, and Light, 1969; Yong, 1969; Marshall and Nongngork, 1970),

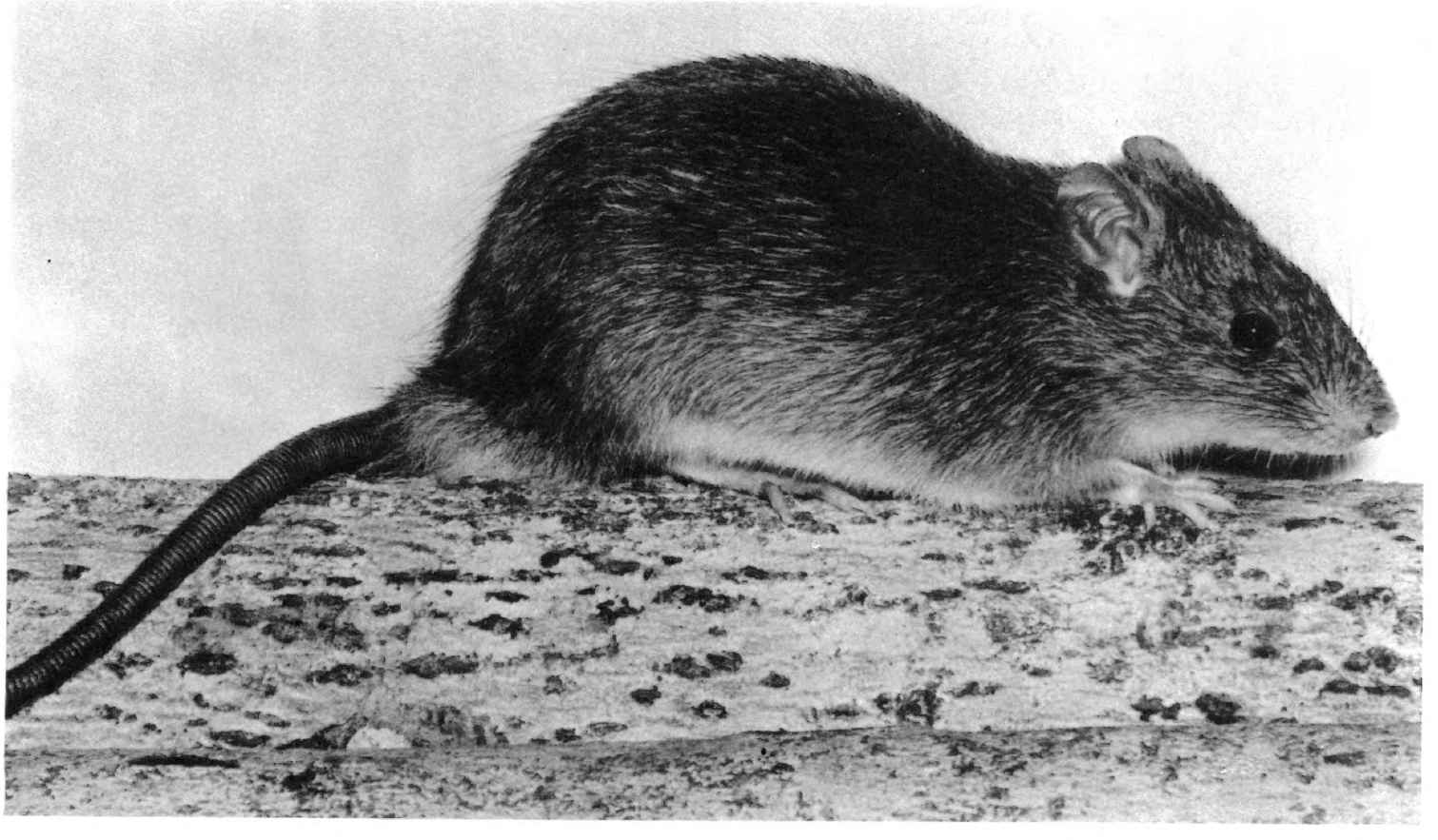

FIG. 1. *Rattus argentiventer*. An adult male caught in experimental rice plot, Kasabart Agricultural University, Bangkok, Thailanc Photographed by Boonsong Lekagul.

although Misonne (1969, p. 144) still views the taxa as representing three ecological subspecies of *R. rattus*. On the basis of chromosomal evidence, Yong (1969) has gone even further and suggested that the taxon *diardii* represents a valid species rather than a subspecies of *R. rattus*, but in my opinion the evidence is insufficient and inconclusive to support this view. Finally, Medway and Lim (1966) believed that the oldest name for the Malaysian wood rat is *tiomanicus*, not *jalorensis*.

External and Cranial Features

Rattus argentiventer is a handsome animal (fig. 1) with a chunky body and short tail. External measurements of 15 adults from Sumba Island are (means and extremes, respectively): length of head and body, 198.3, 176–230; length of tail, 185.7, 172–201; percentage of tail length to length of head and body, 93.9, 84–102; length of hind foot, 36.9, 35–40; and length of ear, 21.8, 20–24.

Pelage of the upper parts of head and body consists of underfur, overfur, translucent and flattened spinelike hairs, and guard hairs. In most specimens the spinelike hairs are thin and flexible, so the pelage is soft and sleek to the touch. Guard hairs are short, inconspicuous, and extend only about one-third of their lengths beyond the overfur. Overall color of the upper parts is yellowish brown speckled with black, a salt and pepper effect. Some specimens have more grayish hues, others are darker and richer with more yellowish and brown hues; the salt and pepper effect, however, is distinctive and characteristic of every specimen. Sides of the head and body are paler than the head and back and the cheeks are gray. In front of each ear is a tuft of orange hairs that contrast conspicuously with color of the head in juveniles and young adults, but are inconspicuous in adults. Throat, axillary, and inguinal regions are white and the remainder of the underparts are silvery gray (the hairs are pale gray basally and white distally). The midventral region of thorax and abdomen is usually darker, in some cases a buffy brown. Some specimens from Sumatra and Celebes are washed with pale yellow or buff; however, these hues may represent discoloration. Upper surfaces of front and hind feet are about the same color as sides of the head and body, and most specimens have a dark brown patch or streak on the carpal and tarsal areas.

The tail is dark brown above and below. In most specimens the tail is shorter than the length of head and body, but in a few it is either the same or slightly longer.

Females have 12 mammae: one pectoral pair, two postaxillary pairs, one abdominal pair, and two inguinal pairs.

Two specimens from Krian, Perak State, Malaysia, in the collection of

the National Museum, Singapore, are albinistic and are the only such examples I have encountered among the several hundred specimens of *R. argentiventer* I examined. NMS 3716, an adult male, is an albino. Pelage of its upper parts and underparts is white. The feet, tail, and ears are unpigmented. The label attached to the study skin bears the notation: "eyes red." The other specimen, NMS 3717, also an adult male, is partially albinistic. Upper parts are pale blond, underparts are white, and tail, feet, and ears lack pigment.

The combination of speckled, yellowish brown upper parts, orange ear tufts in young animals, silvery gray underparts, a short tail relative to length of head and body, and six pair of mammae are distinctive external features of *R. argentiventer* that easily distinguish the species from all named forms of wood rats, *R. tiomanicus*, or house rats, *R. rattus*, occurring in the same geographic areas as *R. argentiventer*. Wood rats, for example, have solid, olive-brown upper parts and either pure or dull white underparts. Females have 10 mammae—one pectoral pair, one postaxillary pair, one abdominal pair, and two inguinal pairs. House rats have brown upper parts; either white, cream, grayish brown, or dark, buffy brown underparts; a tail that is conspicuously longer than length of head and body; and 10 mammae. In some individuals and particular populations of house rats, either one or both of the postaxillary mammae may be twinned and the rats will have 11 or 12 teats. In these animals each of the twinned postaxillary mammae consists of two teats, spaced from 3 to 6 mm. apart. In specimens of *R. argentiventer*, the second pair of postaxillary mammae is invariably 10 to 15 mm. behind the first pair—they are obviously a different pair and not a twinning of the more anterior first pair.

Young of *R. tiomanicus* and *R. rattus* either do not have the bright orange tuft of hairs in front of the ears or this tuft blends with the color of upper parts and is therefore inconspicuous. Thus, the prominent orange tuft in front of the ears in *R. argentiventer* (originally pointed out to me by Barbehenn, who has worked with samples of *R. argentiventer* from the Philippine Islands) will distinguish juveniles and most young adults from individuals of the other two species.

Rattus argentiventer can also be distinguished from *R. tiomanicus* and *R. rattus* by morphology of pads on soles of the hind feet (fig. 2). Shapes of the feet and digits are similar in all three species and all three have six pads: four interdigital pads and two plantar pads—a long, kidney-shaped one and a smaller, circular outer pad. *Rattus rattus* and *R. tiomanicus* are closely similar in morphology of foot pads and in both species the pads are larger and more prominent than those in *R. argentiventer* of comparable age. Furthermore, in *R. rattus* and *R. tiomanicus* the outer plantar pad is large

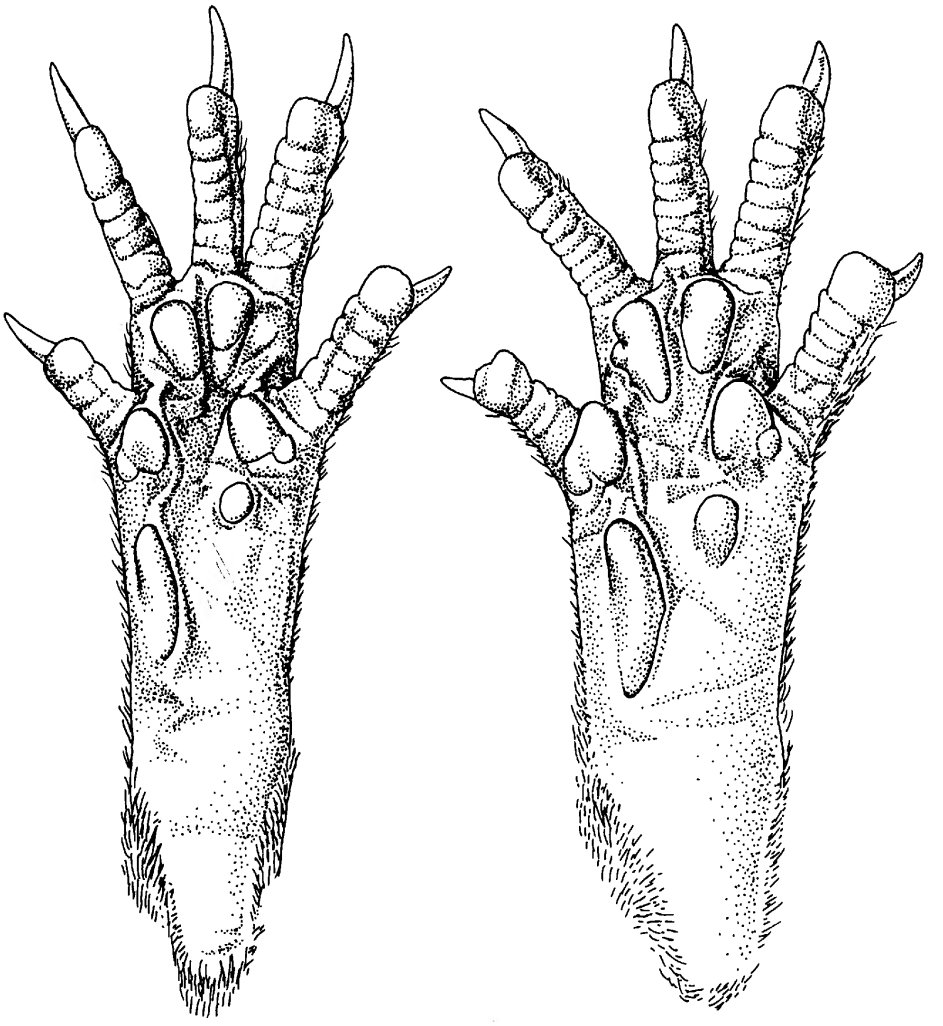

FIG. 2. Plantar views of left hind feet. *Left: Rattus argentiventer* (AMNH 240446, adult male) from Malaya, Selangor, Sungei Tua. *Right: R. rattus diardii* (AMNH 217649, adult female) from Malaya, Selangor, Bukit Mandol. Approximately ×3.5.

and conspicuously raised above the surrounding surface, about half the size of the pad in front of it, and about 2 mm. behind it. In *R. argentiventer* this plantar pad is small and only slightly raised above the surrounding surface, about one-fourth the size of the fourth interdigital pad, and lies just behind it. In specimens at hand, it varies in position from directly behind (and touching its edge in some specimens) to a spot 1/2 to 1 mm. behind the fourth pad.

Transverse and semicircular lamellae (not drawn in fig. 2) adorn

surfaces of the four interdigital and two plantar pads, as well as tips of the digits beneath the claws. In *R. rattus* and *R. tiomanicus* the lamellae are comprised of prominent low ridges. Foot pads of *R. argentiventer* are almost smooth and lamellae are indicated only by shallow striations. *Rattus rattus* and *R. tiomanicus* are terrestrial and scansorial; in fact, they are excellent climbers. The prominent pads of their feet are used to grab twigs and the lamellae provide adhesion. In contrast, *Rattus argentiventer* is primarily terrestrial and a very poor climber. Its foot pads are relatively smaller and the lamellae are low or absent.

External comparisons I discussed in preceding pages are based on my examination of study skins, but the distinctive characteristics of each species can also easily be seen in living animals. Through the efforts of Dr. Illar Muul and his team at the Institute of Medical Research, Kuala Lumpur, Malaysia, I was able to examine live, freshly trapped examples of *R. argentiventer*, *R. tiomanicus jalorensis*, and *R. rattus diardii*. The living examples of each species are more easily distinguished from one another than are study skins. The robust body and short tail of live ricefield rats, along with the distinctive color of their upper parts and underparts are enough to separate them from live examples of the other two species almost at a glance.

The cranium of *R. argentiventer* is best described in comparison with that of *R. rattus*. In figures 4 and 5 a specimen of house rat (*R. rattus pelalae*) from northern Celebes is contrasted with an adult of comparable age of *R. argentiventer* from the island of Bali. Basic distinctions between the two species that are described below will also distinguish all named forms of house rats from samples of *R. argentiventer* that occur in other geographic regions.

Crania of *R. argentiventer* appear more robust than those of *R. rattus* of comparable age. The rostrum is shorter, wider, and deeper (at the level of the anterior edges of the zygomatic plates), and curves conspicuously downward. The interorbital region is narrower. The braincase is oval rather than square. Supraorbital ridges bounding the frontals are not so high and massive as those in *R. rattus*. The interparietal bone is squat, being longer and narrower relative to those in crania of *R. rattus*. The diastema is short and incisive foramina are long and wide. Posteriorly they terminate near the first lingual root of each first upper molar, a point much farther back than the end of the foramina in *R. rattus*. The palatal bridge is shorter and narrower, and the mesopterygoid fossa is narrower. Bullae are larger and more inflated, not only actually, but also relative to size of the skull. Topography of the teeth of *R. argentiventer* resembles that of

R. rattus, but the cusps are better defined and the teeth are wider and appear heavier and more massive.

Chasen (1933), Harrison (1957b), and Medway (1969) provided other morphological distinctions between *R. argentiventer*, *R. rattus*, and *R. tiomanicus*.

Geographic Distribution

The following geographic distribution is based on specimens I have examined and identified as *R. argentiventer* that are in collections of museums and other scientific institutions. Because I am more interested here in the broad geographic distribution of *R. argentiventer* I have only listed institutions where specimens I studied are housed. Specific localities and catalogue numbers of those specimens are on file at the American Museum of Natural History.

SOUTHEAST ASIA
- South Vietnam (specimens in BM, MNHN, and USNM)
- Thailand (specimens from western and peninsular Thailand in ASRCT, AMNH, FTMB, NMS, SMRL, and USNM; including Koh Samui, the largest island off the east coast of the Malay Peninsula)
- Malaya (specimens in AMNH, BM, NMS, and USNM)

GREATER SUNDA ISLANDS
- Sumatra (specimens in BM, MZB, RMNH, and ZMA)
- Borneo (specimens in MZB and USNM)
- Java (specimens in AMNH, BM, MNHN, MZB, NMS, RMNH, USNM, and ZMA; including Kangean Island off the northeast corner of the coast of Java in the Java Sea, specimens in BM)
- Bali (specimens in AMNH, MZB, NMS, RMNH, and USNM)

LESSER SUNDA ISLANDS
- Lombok (specimen in MZB)
- Sumbawa (specimens in MNHN and MZB)
- Komodo (specimens in MZB)
- Rintja (specimen in MZB)
- Flores (specimens in BM, MZB, and RMNH)
- Sumba (specimens in MZB and RMNH)
- Timor (specimens in MZB)

CELEBES (specimens in BM and MZB)

PHILIPPINES (specimens in AMNH, BM, and USNM, from the islands of Mindoro and Mindanao)

NEW GUINEA (specimens in MZB)

Habitat

Habitat of *Rattus argentiventer* is primarily fields of rice and grassland, but the rats have also been found in plantations of oil palms. In Java, for

example, where the species is common and has been extensively studied in connection with programs to control its depredations on rice, Van Heurn (1931, p. 28) summarized his experience with habitat of the ricefield rat by stating that "as long as there is no paddy growing the rats roam about everywhere and during daytime seem to congregate in burrows and crevices in the slopes of dikes and of rivulets, in roadsides, etc. After rice is planted, the wandering rats invade the ricefields to feed on the growing rice by eating the interior of the stem bases and make numerous burrows in the narrow dams that keep the water on the fields. The majority of these burrows serve only as a temporary shelter and a relatively small number only are destined for breeding purposes." Van Heurn also provided excellent photographs of ricefields and dikes in which he found *R. argentiventer* living (1931, pls. 5–7).

In Malaya, *R. argentiventer* also lives in fields of rice under conditions similar to those described in Java (Chasen, 1933; Harrison, 1957; Wood, 1971a), but it has been studied more intensively in grassland and scrub. Harrison (1951, p. 675) stated that in Malaya *R. argentiventer* "is sharply restricted to ricefields (where it is a major pest) and to areas of wasteland covered with the tall grass *Imperata cylindrica* (locally called lallang). This grass dominates well-defined areas which are often perpetuated by burning, a process which removes competing plants but leaves the underground rhizomes of the grass undamaged. If burning and clearing are avoided the area regenerates through scrub to secondary forest. The rat seems to be confined to the grassland stage of the series, and disappears as soon as the grass is strongly mixed with shrubs. It seems also very sensitive to interference, such as trampling, and is very easily trapped out of an area."

Although fields of rice and grassland appear to be the main habitat in which *R. argentiventer* is found, it also frequents plantations of young oil palms, at least in Malaya. For example, in a report of the extent of vertebrate attacks on plantations of oil palms in West Malaysia, Wood (1969, p. 172) recorded that *Rattus tiomanicus* is a major pest in oil palm estates, but that *R. argentiventer* also damages the young oil palms. He wrote: "The ricefield rat, *Rattus argentiventer*, is normally considered to be a pest of rice and an inhabitant of *lallang*. Recently, extremely severe infestations have been found in certain oil palm estates in the Klang area. There seem to be two main conditions necessary for this rat to be able to predominate over *R. tiomanicus* in oil palms. The first is that the palms must not be too tall, since it is apparently less adept at climbing than is *R. tiomanicus*. Thus, on estates where it occurs, it appears to be at its most serious in fields from 3 to 4 years old, where there are fruit bunches but where they are not yet far off the ground. The second condition seems to be a need for a fairly

FIG. 3. Habitat of *Rattus argentiventer*. Field of rice at Saket, Samui Island, Thailand. Photographed by Somsak Pantuwatana.

light loamy soil in which it can burrow, since it is, unlike *R. tiomanicus*, a subterranean dweller." Wood also noted that *R. argentiventer* feeds mostly on the flowers of the oil palms and young bunches of the fruit.

Rattus argentiventer is essentially an animal of the lowlands. Most specimens that I have examined were collected from near sea level to altitudes of 500 to 700 meters. An example of a lowland habitat on the island of Samui from which a specimen of ricefield rat was trapped is shown in figure 3. A few specimens (from South Vietnam and the island of Flores) have been taken at about 1000 meters and the highest record is documented by Lim and Heyneman (1968) who reported taking a specimen from scrub at 1600 meters on the southwest slope of Mount Kinabalu, northern Borneo.

FOOD

Rattus argentiventer is omnivorous. In addition to flowers of oil palms, fruits, nuts, leaves, shoots and roots, growing rice plants and the ripening grain, about half of its diet consists of insects—especially grasshoppers

obtained from fields of rice, and termites and ants taken in grassland and scrub—land snails and slugs, and occasionally lizards (Chasen, 1933; Harrison, 1954, 1961a; Lim, 1966; Lim and Heyneman, 1968; Wood, 1971a).

Other Biological Aspects

Information on other aspects of the biology of *R. argentiventer*, namely reproduction, growth, and survival (Harrison, 1951, 1955), extent of home ranges (Harrison, 1957a, 1957b, 1958), load of ectoparasites and endoparasites (Harrison and Audy, 1951; Dunn, Lim, and Yap, 1968; Lim and Heyneman, 1965; Lim, Ow-Yang, and Lie, 1965; Ow-Yang, 1971), number and morphology of chromosomes (Yong, 1969; Duncan and Van Peenen, 1971), has been compiled mostly for samples of the species from Malaya (although Duncan and Van Peenen, 1971, documented chromosomal morphology of specimens that were obtained from South Vietnam); very little is known about biology of populations in other geographic areas where the species occurs.

Scientific Names Associated with *Rattus argentiventer*

During 1916 to 1945, seven names were proposed in the mammalogical literature for populations that are now recognized as *Rattus argentiventer: argentiventer*, originally described from Sumatra; *brevicaudatus*, applied to rats from Java; *bali*, referring to populations from the island of Bali; *pesticulus*, known by a specimen from Celebes; *saturnus*, applied to rats on Sumba; *chaseni*, originally described from Malaya; and *umbriventer*, which refers to rats from Mindoro in the Philippines. Three of the taxa, *argentiventer*, *brevicaudatus*, and *bali*, were originally listed by Ellerman (1941) as valid subspecies of *R. rattus*, but Chasen (1940), in his handlist of Malaysian mammals, regarded *brevicaudatus* and *bali* as synonyms of *R. r. argentiventer*, an arrangement that was later also used by Ellerman (1949) in his modified arrangement of taxa within the genus *Rattus*, Laurie and Hill (1954) in their list of mammals of New Guinea and nearby regions, and Schwarz and Schwarz (1957), in their monograph on the genus *Rattus*. Hill (1960) went further and provisionally included *chaseni*, as well as *brevicaudatus* and *bali*, as synonyms of *R. r. argentiventer*, allocations that had been previously suggested by Harrison (1957b). Sody (1941), on the other hand, regarded the taxa *argentiventer*, *brevicaudatus*, *bali*, *saturnus*, and *chaseni* to be valid subspecies of *R. rattus*, and he grouped these forms together into his "Argentiventer-section." The taxa *pesticulus* and *umbriventer* have never been associated with *argentiventer* in the published literature. David H. Johnson (according to Barbehenn) was the first person to recognize that

the holotype of *umbriventer* was an example of *R. argentiventer*. I subsequently studied the holotype and was able to verify Johnson's identification. The association of *pesticulus* with *argentiventer* is documented in the present report. A brief history of the names follows.

The taxon *argentiventer* was named and described in 1916 by Robinson and Kloss on the basis of an old male obtained from Pasir Ganting, on the coast of West Sumatra. The holotype is now in the British Museum and registered as number 19.11.5.89. Robinson and Kloss proposed *argentiventer* as a subspecies of "*Epimys rattus*." The generic name *Epimys* was used then for species that are now placed in the genus *Rattus*. Those two authors did not recognize the specific distinctness of the animal they had described nor were they really certain of the distinguishing characteristics of the taxon, for they later misidentified specimens that were referable to *argentiventer*. In 1919, for example, they reported on a collection of mammals obtained from the Bencoolen and Palembang Residencies in southwestern Sumatra. They identified eight rats collected by E. Jacobsen from Suban Ajam, Redjang, Bencoolen as "*Rattus rattus neglectus*?" and commented that "though, however, they have greyish underparts we do not think they have anything to do with our recently described *R. r. argentiventer*." These eight specimens are now in the collection at the Rijksmuseum van Natuurlijke Historie in Leiden (EJ 117–120, 122, and 124–126), and all are examples of *R. argentiventer*, an identification I made when I worked in Leiden in 1969.

In 1918 (p. 67), Horst and Raadt coauthored a paper on the identity of *Mus diardii*, a taxon named and described in 1880 by Jentink and based on a specimen from western Java. Those authors pointed out that three distinct types of *R. rattus* occurred on Java, the house rat, the field (wood) rat, and the ricefield rat, and then they proposed the name *R. r. brevicaudatus* for the ricefield rat ("Indische sawahrat") of Java. Apparently no holotype was designated.

Then in 1921 (p. 123), the taxon *bali* was named and described by Kloss. The taxon was based on seven specimens from Laboean Amok, Kloengkoeng, and Boeleling, on the island of Bali. Kloss did not set apart a holotype, but designated two cotypes, a male from Laboehan Amok and a female from Kloengkoeng. Both specimens are in the Rijksmuseum van Natuurlijke Historie and bear the registration numbers 9805 and 9806, respectively. Both are adults and are examples of *Rattus argentiventer*.

The taxa, *saturnus* and *chaseni*, were named and described by Sody in 1941 (p. 269) as subspecies of *R. rattus*, although he listed them in his "Argentiventer-section" of the genus. *Rattus rattus saturnus* was based on an adult female obtained from Melolo on the island of Sumba and *R. r.*

chaseni was based on an adult male from Krian, Perak, in the Malay States. The holotype of *R. r. saturnus* (MZB 4943) is now in the Rijksmuseum van Natuurlijke Historie and that of *R. r. chaseni* (BM 47.1445) is in the British Museum. Both specimens are examples of *R. argentiventer.*

Rattus argentiventer from the Philippines was first known under the name *R. r. umbriventer*, named and described by Kellogg in 1945 (p. 121). The holotype (USNM 277675), an adult male, and other specimens were obtained from the island of Mindoro. Kellogg was unaware of the true identity of the taxon he had described, but he did recognize that the form had distinctive external features, for he remarked that "this rat is readily distinguished from other rats in this section of the genus by the coarse ticking of the upperparts and the color pattern of the underparts. A similar distribution of light and dark areas on the underparts occurs occasionally in other members of the *Rattus rattus* section." The holotype and most of the other specimens in the series examined by Kellogg are examples of *R. argentiventer.*

The other name that can be associated with *Rattus argentiventer* is *R. pesticulus* from Celebes.

THE ASSOCIATION OF *RATTUS PESTICULUS* WITH *RATTUS ARGENTIVENTER*

Rattus pesticulus was named and described by Oldfield Thomas in 1921 and was based on a specimen obtained in 1908 from Menado, northeastern Celebes. It was originally deposited in the former Zoological Museum at Buitenzorg, Java (now the Museum Zoologicum Bogoriense at Bogor) and subsequently sent to Oldfield Thomas by the director, K. W. Dammerman, for identification. Thomas considered the specimen to be a pygmy member of the "*rattus-neglectus* group" and described it as "size very small, hardly greater than in the *concolor* group. Fur thin and coarse, not definitely spinous. General colour above dull reddish brown, sides rather greyer, under surfaces sharply defined white, the hairs on the throat with grey bases. Hands and feet white. Tail of medium length, thinly haired, light brown, almost white basally. Mammae 3–3 = 12. Skull conspicuously smaller in all dimensions than in *neglectus*, but of about the same general proportions. Supraorbital beads distinct; no post-orbital projections. Palatal foramina to the level of the front root of m^1. Bullae of normal size."

From the time that Thomas's original description was published until 1936 no other specimens had been allocated to *R. pesticulus* in the mammalogical literature. In 1936 in his paper on the Muridae of the Indo-Australian region Tate included *R. pesticulus* in his "*Rattus rattus* group." His knowledge of the taxon was based on the original description and

three specimens in the Archbold Collection of the American Museum of Natural History (AMNH 101275, 101277, and 101278) from Roeroekan, northeastern Celebes that he identified as *R. pesticulus* (p. 530). Tate was unsure about his identification of these specimens and pointed out that their measurements were larger than those published for the holotype of *R. pesticulus*, and that the animals possibly represented one of the Bornean subspecies of *R. rattus*. He also indicated that his specimens had the same number of mammae as in the holotype of *R. pesticulus*. I examined the three rats and found them to be house rats, *R. rattus*. Furthermore, the females have 10 mammae, not 12, the same number as in the holotype of *R. pesticulus*.

From 1936 to the present, I know of no other specimens, either in the literature or in collections of museums, that have been identified as *R. pesticulus* and the morphological and ecological characteristics of the population it represents have remained poorly known. Despite this ignorance the taxon has been differently allocated at least three times from 1936 to 1961. In 1941 Ellerman listed *pesticulus* as a species of *Rattus* and included it within his "*rattus group*" (p. 182). In 1949 he regarded *pesticulus* as a subspecies of *R. rattus* (p. 61), an allocation that was followed by Laurie and Hill (1954, p. 101) in their list of mammals of New Guinea, Celebes, and adjacent areas.

So, previous to 1961 the taxon *pesticulus* was invariably associated with *R. rattus*, either as a species within the *Rattus rattus* group, or as a subspecies of *R. rattus*. Schwarz (1961) presented a radically different opinion regarding the identity and allocation of *R. pesticulus*. He examined the holotype at the British Museum and concluded that it was identical with *R. musschenbroekii*. That species is a rat of small body size that occurs on Celebes and is morphologically far removed from the *R. rattus* group. Ellerman, for example, had placed it in a different subgenus than *R. rattus* and its allies. He considered *R. musschenbroekii* to belong in the subgenus *Apomys* (1949, p. 73), a name that was later replaced by *Lenothrix* (Ellerman and Morrison-Scott, 1951). The most recent opinion regarding the allocation of *R. musschenbroekii* is that of Misonne (1969) who placed the species in the genus *Rattus* under the subgenus *Leopoldamys*.

In 1969 I pointed out that Schwarz's allocation was incorrect, that *R. pesticulus* had nothing to do with *R. musschenbroekii*, and that it was more closely allied to species in the subgenus *Rattus* (Musser, 1969). My opinion was based on Thomas's original description and a photograph of the skull of the holotype taken by Tate when he visited the British Museum in the 1930s. I did not have enough other data at that time to clearly identify and properly allocate the taxon. Since then I have measured and studied

the holotype of *R. pesticulus*; its identity is documented below.

The holotype of *R. pesticulus* (BM 21.2.9.11) is a young adult female and consists of a study skin with cranium and mandibles. External measurements taken by me from the dry skin are: length of head and body, 155; length of tail, 148; length of hind foot (including the claw), 31; and length of ear from notch, 13. The skull is complete and in good condition and the teeth are moderately worn.

Thomas's description of the animal was accurate. The specimen is about the size of an adult *R. exulans*. Pelage of its upper parts is coarse, thin, and reddish brown. Underparts are white and washed with a tinge of pale, grayish buff. The tail is straw yellow and the hands and feet are whitish. The specimen has 12 conspicuous mammae. The coloration described by Thomas and so evident now in the holotype represents alteration of the original hues owing to initial preservation of the specimen in fluid and subsequent preparation as a dry study skin. This was verified by John Edwards Hill of the British Museum who told me that the material Dammerman had sent to Thomas was assuredly originally preserved in fluid. The reddish brown of the upper parts is clearly discoloration and the whitish hands and feet and yellowish tail are the results of bleaching. This color alteration is typical of many old specimens in museums that were originally preserved in fluid and later made into study skins.

Because the pelage is discolored, that feature of the holotype of *R. pesticulus* cannot be used to determine its affinities. The other external characteristics that are more reliable, namely the relative length of tail—about as long as the head and body—and the six pairs of mammae point to *R. argentiventer*, an identity verified by cranial features. The skull is a young adult of *R. argentiventer* and it is similar in size and configuration to other specimens of *R. argentiventer* of comparable age from Celebes and regions outside of that large island.

Rattus argentiventer was first recorded from Celebes by Sody in 1941 (p. 268) in his report on the murids from the Indo-Malayan and Indo-Australian regions that were housed at the Zoological Museum in Buitenzorg. Sody identified five specimens that had been obtained at Makassar in the southwest peninsula of Celebes (MZB 3000, and 4876–4879) as *R. r. argentiventer*. Through the courtesy of the staff of the Museum Zoologicum Bogoriense I have been able to borrow and study those specimens. Only three of the five rats are examples of *R. argentiventer:* MZB 3000, collected July, 1931, and MZB 4878 and 4879, obtained in 1940. The other two specimens, MZB 4876 and 4877, are house rats, *R. rattus*. The three examples of *R. argentiventer* are young adults; MZB 4878 is the largest and oldest and MZB 3000 is the smallest and youngest. Their

cranial measurements are listed in table 1 and the skulls of the two oldest and largest specimens, MZB 4878 and 4879, are illustrated in figures 4 and 5. In those figures they are contrasted with a specimen of the ricefield rat from the island of Bali. That individual is an adult and is much larger than the two young adults from Celebes. The cranial differences that can be seen between those specimens reflect primarily age and individual variations. This magnitude of difference between adults and young adults is typical in samples of *R. argentiventer* that I have studied from throughout its geographic range, including samples from Celebes.

After I completed this manuscript I had the opportunity to visit Bogor and work in the Museum Zoologicum Bogoriense in November of 1971. In that collection I found seven additional specimens of *R. argentiventer* from Celebes that Sody had not recorded in his report of 1941. Three of the specimens (MZB 6412, young adult male; 6413 and 6414, adult males; all collected in 1941) are from the district of Loewoe in west-central Celebes (approximately latitude 2° 15′ S, longitude 120° 15′ E); one example (MZB 4227, young adult female; date of collection unknown) is from Makassar; and three (MZB 9005, adult female; 9006 and 9007, adult males; all obtained on May 8, 1916) are from Boeloekoemba, Balao, Galeong in the southern tip of the southwestern peninsula of Celebes.

The three specimens from Loewoe are in full, bright pelage and are classical examples of *R. argentiventer*. Specimens 6413 and 6414 are the oldest and largest of the series (table 1). Size and configuration of their skulls closely resemble the skull of the specimen from Bali shown in figures 4 and 5. Number 6412 is younger than the two from Loewoe. In size and age, as estimated by wear of teeth and cranial features, it falls between MZB 6414 and MZB 4878, the oldest specimen illustrated in figures 4 and 5. Number 4247, the example from Makassar, is about the same age and size as 4878 (table 1).

The three specimens from Boeloekoemba are poorly preserved. Color of their pelage has been slightly altered, but not to the degree that the diagnostic orange ear tufts and agouti pattern of the upper parts are obscure.

Recently collected specimens of *argentiventer* have been recorded from Celebes. Yosida, Tsuchiya, and Moriwaka (1971) analyzed chromosomes of 29 rats out of a sample of 43 that were obtained from Makassar, Celebes. Those authors identified their specimens as "*R. rattus argentiventer*." I have not seen the material so I cannot verify their identification.

Selected cranial measurements of the holotype of *R. pesticulus* are listed in table 1 and compared there with specimens of *R. argentiventer* from Celebes. Of the examples of *R. argentiventer* from Celebes, MZB 5879 (illustrated in figures 4 and 5) is most like the skull of *R. pesticulus* in size

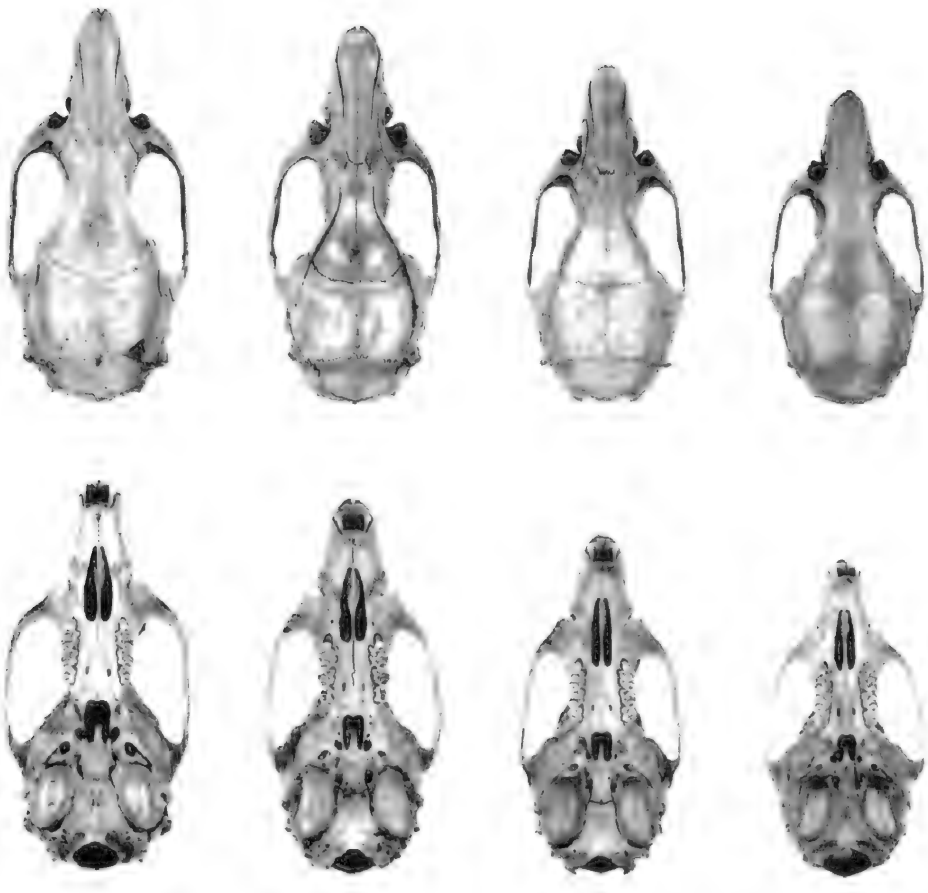

FIG. 4. Dorsal (top) and ventral (bottom) views of crania. *Left to right:* adult (AMNH 153004) *Rattus rattus pelelae*, Boemboelan, northern Celebes; adult (AMNH 107543) *R. argentiventer*, Oeboed, Bali; and two young adult (MZB 4878 and 4879, respectively) *R. argentiventer*, Makassar, southwestern Celebes. All ×1. Photographed by Robert E. Logan.

and in configuration. In my opinion, the holotype of *R. pesticulus* is clearly an example of *R. argentiventer*.

At the present time I see no reason to maintain the name *pesticulus* as valid for samples of *R. argentiventer* from Celebes. Morphological features of the holotype of *pesticulus* that can be used for comparison with other samples do not differ in any important way from specimens of comparable age from Makassar. In turn, those individuals, as well as the specimens from Loewoe and Boeloekoemba, are closely similar to specimens of *R. a. argentiventer* of comparable age that I have examined from Sumatra.

Samples of *R. argentiventer* from Celebes are small and most biological

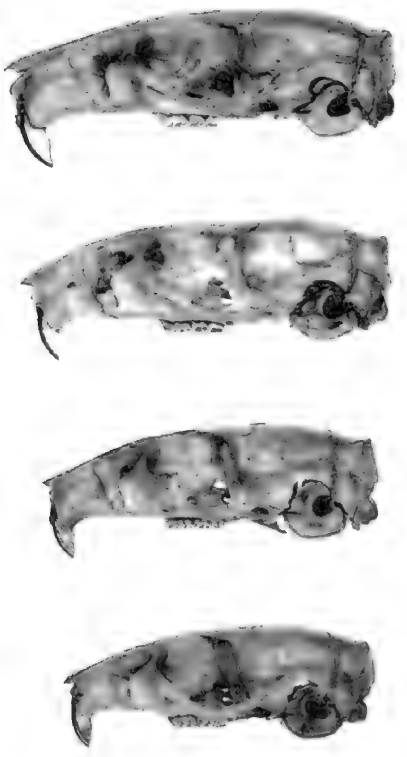

FIG. 5. Lateral views of the same crania that are illustrated in figure 3. From *top to bottom: Rattus rattus pelelae*, Boemboelan; *R. argentiventer*, Oeboed; and the two *R. argentiventer* from Makassar. All ×1. Photographed by Robert E. Logan.

aspects of the population from there are unknown. For example, the only information on habitat of the species in Celebes comes from a label attached to one of the females (MZB 3000) collected at Makassar. On it is the notation that the animal came from a dike in a field of rice.

RATTUS ARGENTIVENTER FROM NEW GUINEA

When he recorded *Rattus argentiventer* from Celebes, Sody (1941) also noted a specimen from New Guinea that was in the Zoological Museum at Buitenzorg (Bogor). It was probably this record that prompted Laurie and Hill (1945) to list *R. argentiventer* as possibly occurring in New Guinea. When I first read Sody's account I thought the specimen he referred to may have been an example of *R. gestri*, for that species is common in the lowlands of New Guinea, it is superficially similar to *R. argentiventer* in external and cranial features, and the females also have 12 mammae. Since then I have been able to borrow the rat from the Museum Zoologicum Bogoriense.

The specimen (MZB 4875) is a young adult female and consists of a poorly made study skin and almost complete cranium and mandibles. The pelage is discolored; upper parts are now reddish brown and the under-

TABLE 1

CRANIAL MEASUREMENTS (IN MILLIMETERS) OF THE HOLOTYPE OF *Rattus pesticulus* AND SPECIMENS OF *Rattus argentiventer* FROM CELEBES AND NEW GUINEA

Measurement	*R. pesticulus*	*R. argentiventer*						
		Celebes						New Guinea
	BM 21.2.9.11	MZB 6413	MZB 6412	MZB 4227	MZB 4878	MZB 4879	MZB 3000	MZB 4875
Greatest length of skull	37.5	46.5	41.7	39.0	39.5	37.1	35.6	—
Zygomatic breadth	18.2	—	19.6	18.7	19.2	18.5	—	—
Interorbital breadth	5.5	6.6	5.8	5.6	5.7	5.3	5.0	5.4
Length of nasals	13.2	17.8	14.8	14.0	14.2	12.6	12.2	12.5
Length of rostrum	10.9	14.4	12.5	12.1	11.7	10.5	10.3	10.2
Breadth of rostrum	6.7	9.0	7.7	7.3	7.5	6.7	6.1	7.0
Breadth of braincase	15.0	16.8	15.5	15.5	15.3	14.9	14.6	15.0
Height of braincase	11.1	—	11.0	10.9	10.9	10.6	10.1	—
Breadth of zygomatic plate	4.1	5.7	5.1	4.9	4.8	4.5	4.0	4.0
Length of diastema	10.2	13.3	11.2	10.2	11.0	9.1	9.3	9.4
Length of incisive foramina	7.0	8.8	9.2	8.1	7.8	7.1	6.9	6.9
Breadth of incisive foramina	2.4	3.3	2.5	2.5	2.4	2.4	2.3	2.4
Palatal length	20.7	25.4	—	21.0	22.0	19.8	19.4	19.5
Length of palatal bridge	7.5	9.1	—	7.4	7.7	7.7	7.1	7.3
Breadth of mesopterygoid fossa	2.4	2.5	2.0	2.1	2.5	2.2	—	2.4
Alveolar length of M^{1-3}	6.8	8.2	8.1	7.8	7.3	7.6	7.0	7.1
Length of M^1	3.2	3.6	3.8	3.7	3.4	3.5	3.4	3.3
Breadth of M^1	2.0	2.4	2.4	2.4	2.1	2.2	2.1	2.2
Length of bulla	6.5	—	7.8	7.6	7.7	7.3	7.0	7.0

parts are dirty, creamy yellow. A faded, orange tuft is present in front of each ear. The specimen has 12 well-developed and conspicuous mammae. The skin is that of a young *R. argentiventer* in which the original pelage color has been altered. Size and configuration of the skull is similar to that of the two youngest specimens of *R. argentiventer* from Celebes, MZB 3000 and 4879 (table 1). Sody had correctly identified the rat from New Guinea.

The specimen was collected on June 7, 1910, from Tanah Merah (latitude 6° 12′ S, longitude 140° 14′ E), a small town on the east side of the Digul River in the tropical coastal plain of southern West Irian, New Guinea. There is no information available about the habitat in which the animal was caught.

When I was working in the museum at Bogor, I located five additional specimens of *R. argentiventer* that had been obtained in New Guinea. All are juveniles and were collected on June 7, 1910 from Tanah Merah, the same time and place as the young adult discussed above. Two of the specimens are females (MZB 4196 and 4198), one is a male (MZB 4195), and the other two could not be sexed (MZB 4197 and 4199). Sody had originally identified and recorded these specimens as *Rattus rattus septicus* (Sody, 1941), but all are juvenal examples of *R. argentiventer*. They have dirty, creamy yellow underparts and reddish brown upper parts, but the color is an alteration, like that seen in MZB 4875, that is typical of old specimens of *R. argentiventer*. All the specimens have some trace of orange in front of the ears and these tufts are particularly conspicuous on 4198 and 4195. I could not locate all pectoral and pelvic mammae on the two females because of the way the skins were prepared, but I did find that each specimen has two pairs of postaxillary mammae as is typical of *R. argentiventer*. They are definitely two distinct pairs—the second pair is 10 mm. posterior to the first pair—and not a twinning of one pair of postaxillary mammae as is sometimes found in series and individual specimens of *R. rattus*. Skulls of the five specimens are like those of juvenile *R. argentiventer* from regions outside of New Guinea.

There are other specimens of *Rattus* from Tanah Merah, and these were collected in 1959 during an expedition by the Dutch who explored the mountainous central portion of what was then Netherlands New Guinea. The party spent some time in Tanah Merah, and Brongersma and Venema (1963), who reported on the expedition, wrote that "Tanah Merah, a very quiet spot, situated three days' sail from the mouth of the Digul, was originally an internment camp, built about thirty years ago on the red clay which gave it its name. At that time it had no airfield. Once every three months a tiny steamboat arrived with the necessary supplies for the internees and their guards, and for the small garrison which, ravaged by

malaria and blackwater fever, led a monotonous existence in the stifling atmosphere of the steaming hot jungle." Personnel of the expedition collected mammals in and around the town and these specimens are now in the collection of the Rijksmuseum van Natuurlijke Historie at Leiden. They obtained 103 rats from Tanah Merah and I examined them carefully with the thought that some of them might be examples of *R. argentiventer*. All, however, are house rats, *R. rattus*.

DISCUSSION

The murid fauna of Celebes is rich in number of species and most of them are in the genus *Rattus*, as that genus is defined by Ellerman (1941, 1949). Laurie and Hill (1954), for example, recognize more than 60 taxa of *Rattus* from Celebes. Many of those represent valid species, some are identical with other taxa, and the identities and allocations of a few are uncertain. Three objectives of my study of *Rattus* on Celebes have been to detect the number of valid species occurring on that island; then to assess their zoogeographic relationships with murid faunas of the Asian mainland and islands on the Sunda Shelf to the west, the Philippine Islands to the north, the Lesser Sunda Islands to the south, and the land masses in the Indo-Australian region to the east; and to determine the number of species that are actually native to regions outside of Celebes that have been transported there by humans. My first step in this study has been to define morphological and, if possible, ecological limits of each species that occurs on Celebes and to associate the oldest and valid taxonomic name with it. In doing so I have found that the number of species of *Rattus* that have been introduced into Celebes has been underestimated. Until the named forms that are associated with these introduced species are identified, they confuse our understanding of the zoogeography of native *Rattus* on Celebes.

During the period when the taxon *argentiventer* was linked to *R. rattus* as an "ecological subspecies," and later when it was recognized as a valid species, the form has been considered as either "semi-parasitic on man" (Chasen, 1933) or a "commensal" (Harrison, 1961b). Furthermore, Harrison (1961b) has hypothesized that *R. argentiventer* has spread to at least some of the geographic regions where it now occurs through human activities. I think *R. argentiventer* is one of those species that was inadvertently transported to Celebes by humans. Several data support this view. First, wherever *R. argentiventer* has been found it occupies a habitat that has resulted from modification of the original forest by humans. This association between species and habitat is exemplified by Harrison's (1961b) experience with *R. argentiventer* in Malaya. He wrote, "in large

areas of Malaya the primitive swamp forest has been felled, and the cleared land used for growing rice. In other parts, land cleared but not cultivated has been seized by the cosmopolitan grass *Imperata cylindrica* which is perpetuated by burning. It is these two forms of grassland, ricefields and *Imperata*-grass, that *Rattus argentiventer* inhabits and it will be noted that both habitats are man-made."

Although little is known about the habitat on Celebes from which the specimens of *R. argentiventer* were taken, at least one of the four individuals from Makassar, a seaport in southwestern Celebes, was obtained from a field of rice. Both the northeastern tip and the southwestern peninsula of Celebes consist of ricefields and grassland broken up by patches of primary and secondary forests. Ricefields are also scattered throughout the lowlands of west-central Celebes as well (van Steenis, 1958). Even by the latter part of the 1800s the southwestern peninsula of Celebes had been developed for the growing of rice. Wallace (1872), for example, described how extensively the forests had been cleared in the region around Makassar, and noted that the land had been converted to fields of rice.

Secondly, the samples of *R. argentiventer* from throughout its known geographic range are morphologically similar to one another. There is geographic variation in color of upper parts and underparts in samples I have examined, and some of the samples may represent populations that are morphologically distinct enough to be recognized as valid subspecies when *R. argentiventer* is taxonomically revised, but even so the species is still morphologically distinctive and easily recognizable wherever it has been found. Among species within the genus *Rattus*, the only other species with similar geographic distributions, that is, from the Asian mainland over the Sunda Shelf and Lesser Sunda Islands to the Philippines and New Guinea, are species that were probably spread over this large region mostly by humans. Five species of *Rattus* from Celebes fit this pattern of geographic distribution: *R. argentiventer*, *R. exulans*, *R. norvegicus*, *R. rattus*, and *R. nitidus*. (I will document the geographic distribution of *R. nitidus* in a paper now in preparation. In addition to samples from the Asian mainland, I have examined series of *R. nitidus* from northern Luzon in the Philippines; from Celebes, where it had been described as *R. hoffmani subditivus* Miller and Hollister, 1921; from Ceram, where Thomas, 1920, described it as *R. manuselae*; and from New Guinea, where it was known as *R. vanheurni* Sody, 1933).

In contrast to the five species discussed above, all other species of *Rattus* known from Celebes are indigenous and the information I have been able to gather about their habitats indicates that all of them occur in forests and are rarely taken in such habitats as grasslands, fields of rice, or around

human dwellings. These native species are listed below. Following some of the species are names of taxa in parentheses that represent either synonyms or subspecies. Authors and dates and places of publication of those taxa can be found in Laurie and Hill (1954). The list is based on my studies of the murid fauna of the Indo-Malayan and Indo-Australian regions. Some results of those studies that have focused on *Rattus* of Celebes have been published elsewhere (Musser, 1969a, 1969b, 1970b, 1971a, 1971b, 1971c, 1971d, 1971e) and other results are being prepared for publication. The list is a preliminary one—a few of the taxa may eventually be differently allocated and some will be taken out of the genus *Rattus* and placed elsewhere.

R. dammermani (*toxi*)
R. hoffmanni (*linduensis*, *mengkoka*, *mollicomus*, *mollicomulus*, *tatei*, and *biformatus*)
R. elephinus
R. xanthurus (*faberi* and *paraxanthus*)
R. bontanus
R. marmosurus (*facetus* and *tondanus*)
R. salocco
R. foramineus (*pelurus*)
R. hamatus
R. taerae (*tatei* and *simpsoni*)
R. arcuatus
R. chrysocomus (*nigellus*, *rallus*, *brevimolaris*, *coelestis*, and *koka*)
R. fratrorum
R. adspersus
R. penitus (*sericatus*, *inferior*, and *heinrichi*)
R. andrewsi
R. musschenbroekii (*tetricus*, *lalawora*, and *aspinatus*)
R. hellwaldii (*localis*, *cereus*, and *griseogenys*)
R. dollmani
R. celebensis
R. punicans
R. callitrichus (*maculipilis*, *jentinki*, and *microbullatus*)
R. dominator (*camurus*, *ursinus*, and *frosti*)
R. beccarii

These species of *Rattus* are native to Celebes and its offshore islands, including the Sula Islands, and do not occur elsewhere. Their closest relatives are found primarily on islands of the Sunda Shelf and on the mainland of Southeast Asia; a few occur in the Philippines. The degree of morphological differences between the indigenous species on Celebes and their relatives outside that area is at the level of morphological differentiation that exists between species and between subgenera of *Rattus*. They are not the kind, nor the magnitude, of morphological differences found between local populations of one species, as is the case with *R. argentiventer*,

R. rattus, *R. norvegicus*, *R. nitidus*, and *R. exulans* from the Indo-Malayan and Indo-Australian regions. Set against this pattern of morphological relationships shown by native species of *Rattus* on Celebes, the occurrence of *R. argentiventer* on that large island is zoogeographically anomalous. In my opinion its presence there is best explained by the hypothesis that the species was introduced by humans.

The specimens of *R. argentiventer* from New Guinea represent the introduction of the ricefield rat to an indigenous assemblage of *Rattus* whose close relatives outside of New Guinea occur only in Australia and on some islands in the Moluccas (Tate, 1951; Laurie and Hill, 1954). The other four species of *Rattus* found on New Guinea but not native to that land mass are *R. rattus*, *R. norvegicus*, *R. exulans*, and *R. nitidus*.

ACKNOWLEDGMENTS

I am grateful to the following persons who lent me specimens and allowed me to study material under their care: Dr. A. M. Husson of the Rijksmuseum van Natuurlijke Historie; Mr. John Edwards Hill of the British Museum (Natural History); Dr. Peter J. H. van Bree of the Zoological Museum of the University of Amsterdam; Mr. Eric Alfred of the National Museum, Singapore; Dr. Charles O. Handley, Jr. of the National Museum of Natural History, Smithsonian Institution; Dr. F. Petter of the Musèum National d'Histoire Naturelle; Dr. S. Somadikarta and Mr. Boeadi of the Museum Zoologicum Bogoriense; and Dr. Joe T. Marshall, Jr. of the SEATO Medical Research Laboratory.

I appreciate the fine efforts of Mr. Robert E. Logan, a staff photographer of the American Museum of Natural History, who took the photographs of the skulls in figures 4 and 5; Dr. Boonsong Lekagul, who photographed the rat illustrated in figure 1; and Mr. Somsak Pantuwatana, who photographed the habitat on Samui Island (fig. 3). Miss Jennifer A. Perrott made the excellent renditions of rat feet in figure 2.

Drs. Joe T. Marshall and Illar Muul deserve special mention. Marshall allowed me to use specimens in his laboratory in Bangkok, permitted me access to specimens preserved in other institutions in Bangkok, sent me the photographs used in figures 1 and 3, read and critically evaluated the manuscript, and gave me the benefit of his knowledge about the habitat and geographic distribution of *R. argentiventer* in Thailand.

Dr. Muul took me into the habitat where *R. argentiventer* lives in Malaya and made it possible for me to study the living animal.

Drs. Kyle R. Barbehenn, Karl F. Koopman, Sydney Anderson, and Richard G. Van Gelder read the manuscript and provided critical comments and suggestions that significantly improved its quality. Miss Susan

Loesser, with her usual competence, translated my rough drafts into final manuscript.

Mr. Richard Archbold, of the Archbold Expeditions, the American Museum of Natural History, and the Council of the Scientific Staff of that institution provided financial support for my studies in Europe. My work at the Museum Zoologicum Bogoriense was sponsored by the Celebes Fund of the American Museum of Natural History.

LITERATURE CITED

BRONGERSMA, L. D., AND G. F. VENEMA
1961. To the mountains of the stars. New York, Doubleday and Co., pp. i-xv, 17–318, figs. 1–23, pls. 1–48.

CHASEN, F. N.
1933. On the forms of *Rattus rattus* occurring on the mainland of the Malay Peninsula. Bull. Raffles Mus., Singapore, Straits Settlement, no. 8, pp. 5–24.
1940. A handlist of Malaysian mammals (A systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including the adjacent small islands). *Ibid.*, no. 15, pp. i–xx, 1–209, 1 map.

DHALIWAL, S. S.
1961. Ecological and geographical studies of *Rattus rattus* in Malaya. Jour. Mammal., vol. 42, pp. 349–358, figs. 1, 2, pls. 1, 2.
1962. Studies on body measurements and skeletal variations of two taxa of *Rattus rattus* in Malaya. *Ibid.*, vol. 43, pp. 249–261, 1 fig., 1 pl.
1964. Breeding experiments and pelage differences between two subspecies of *Rattus rattus*. Bull. Natl. Mus. Singapore, no. 32, pp. 31–44.

DUN, F. L., B. L. LIM, AND L. F. YAP
1968. Endoparasite patterns in mammals of the Malayan rain forest. Ecology, vol. 49, pp. 1179–1184, figs. 1, 2.

DUNCAN, J. F., AND P. F. D. VAN PEENEN
1971. Karyotypes of ten rats (Rodentia: Muridae) from Southeast Asia. Caryologia, vol. 24, no. 3, pp. 331–346, figs. 1–12.

ELLERMAN, J. R.
1941. The families and genera of living rodents. London, British Museum (Natural History), vol. 2, Family Muridae, pp. i–xii, 1–690, figs. 1–50.
1949. *Ibid.*, vol. 3, pt. 1, pp. i–v, 1–210.
1951. Checklist of palaearctic and Indian mammals, 1759 to 1946. *Ibid.*, pp. 1–810, 1 map.

HARRISON, J. L.
1951. Reproduction in rats of the subgenus *Rattus*. Proc. Zool. Soc. London, vol. 121, pp. 673–694, figs. 1–6.
1954. The natural food of some rats and other mammals. Bull. Raffles Mus., Singapore, no. 25, pp. 157–165.
1955. Data on the reproduction of some Malayan mammals. Proc. Zool. Soc. London, vol. 125, pp. 445, 460, figs. 1–3.
1957a. Results of mark-recapture experiments on small animals. Malayan

Nature Journal, vol. 12, pp. 82–90, figs. 1–6.

1957b. Habitat of some Malayan rats. Proc. Zool. Soc. London, vol. 128, pp. 1–21, figs. 1–10.

1958. Range of movement of some Malayan rats. Jour. Mammal., vol. 39, pp. 190–206, figs. 1–9.

1961a. The natural food of some Malayan mammals. Bull. Singapore Natl. Mus., no. 30, pp. 5–18.

1961b. Ecology of the forms of *Rattus rattus* in the Malay Peninsula. Proc. Ninth Pacific Sci. Cong., vol. 19, pp. 19–24, 1 fig.

HARRISON, J. L., AND J. R. AUDY

1951. Hosts of the mite vector of scrub typhus. 1. A checklist of the recorded hosts. Ann. Trop. Med. and Parasit., vol. 45, nos. 3 and 4, pp. 171–185.

HARRISON, J. L., AND R. TRAUB

1950. Rodents and insectivores from Selangor, Malaya. Jour. Mammal., vol. 31, pp. 337–346.

HILL, J. E.

1960. The Robinson Collection of Malaysian mammals. Bull. Raffles Mus., Singapore, no. 29, pp. 1–112, figs. 1–4.

HORST, M. D. AND O. L. E. DE RAADT

1918. De identiteit van *Mus diardii* Jentink. Zool. Meded., Rijksmus. Natuur. Hist., vol. 4, pp. 67–69.

KELLOGG, R.

1945. Two new Philippine rodents. Proc. Biol. Soc. Washington, vol. 58, pp. 121–124.

KLOSS, C. B.

1921. Some rats and mice of the Malay Archipelago. Treubia, vol. 2, pp. 115–124, pls. 2–3.

LAURIE, E. M. O., AND J. E. HILL

1954. List of land mammals of New Guinea, Celebes and adjacent islands 1758–1952. London, British Museum (Natural History), pp. 1–175, pls. 1, 2, 1 map.

LIM, B. L.

1966. Land molluscs as food of Malayan rodents and insectivores. Jour. Zool., vol. 148, pp. 554–560.

LIM, B. L., AND D. HEYNEMAN

1965. Host-parasite studies of *Angiostrongylus cantonensis* (Nematoda, Metastrongylidae) in Malaysian rodents: natural infection of rodents and molluscs in urban and rural areas of central Malaya. Ann. Trop. Med. Parasit., vol. 59, no. 4, pp. 425–433.

1969. A collection of small mammals from Tuaran and the southwest face of Mt. Kinabalu, Sabah. Sarawak Mus. Jour., vol. 16, pp. 257–280, 1 fig., pls. 33–36.

LIM, B. L., C. K. OW-YANG, AND K. J. LIE

1965. Natural infection of *Angiostrongylus cantonensis* in Malaysian rodents and intermediate hosts, and preliminary observations on acquired resistance. Amer. Jour. Trop. Med. Hyg., vol. 14, no. 4, pp. 610–617.

MARSHALL, J. T., JR., AND VANDEE NONGNGORK

1970. Mammals of Samui Island, Thailand. Nat. Hist. Bull. Siam Soc., vol. 23, pp. 501–509, figs. 1, 2.

MEDWAY, L.
1965. Mammals of Borneo. Field keys and an annotated checklist. Malaysian Branch of the Royal Asiatic Society Singapore, Malaysia Printers, pp. i–xiv, 1–193, figs. 1–9, pls. 1–34, 1 map.
1969. The wild mammals of Malaya and offshore islands including Singapore. Kuala Lumpur and Singapore, Oxford Univ. Press, pp. i–xix, 1–127, figs. 1–11, pls. 1–15.

MEDWAY, L., AND B. L. LIM
1966. The specific relations of *Rattus tiomanicus* (Miller). Bull. Natl. Mus. Singapore, no. 34, pp. 33–38.

MILLER, G. S., JR., AND N. HOLLISTER
1921. Descriptions of sixteen new murine rodents from Celebes. Proc. Biol. Soc. Washington, vol. 34, pp. 66–76.

MISONNE, X.
1969. African and Indo-Australian Muridae. Evolutionary trends. Mus. Roy. l'Afrique Cent., Tervuren, Zool., no. 172, pp. 1–219, figs. A-K, pls. 1–27.

MUSSER, G. G.
1969a. Results of the Archbold Expeditions. No. 89. Notes on the taxonomic status of *Rattus aspinatus* Tate and Archbold and *Mus callitrichus* Jentink (Rodentia, Muridae). Amer. Mus. Novitates, no. 2365, pp. 1–9.
1969b. Results of the Archbold Expeditions. No. 92. Taxonomic notes on *Rattus dolmani* and *Rattus hellwaldi* (Rodentia, Muridae) of Celebes. *Ibid.*, no. 2386, pp. 1–24, figs. 1–3.
1970a. Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. *Ibid.*, no. 2406, pp. 1–27, figs. 1–6.
1970b. Results of the Archbold Expeditions. No. 93. Reidentification and reallocation of *Mus callitrichus* and allocations of *Rattus maculipilis*, *R. m. jentinki*, and *R. microbullatus* (Rodentia, Muridae). *Ibid.*, no. 2440, pp. 1–35, figs. 1–4.
1971a. Results of the Archbold Expeditions. No. 94. Taxonomic status of *Rattus tatei* and *Rattus frosti*, two taxa of murid rodents known from middle Celebes. *Ibid.*, no. 2454, pp. 1–19, figs. 1, 2.
1971b. The taxonomic association of *Mus faberi* Jentink with *Rattus xanthurus* (Gray), a species known only from Celebes (Rodentia, Muridae). Zool. Meded., Rijksmus. Natuur. Hist. Leiden, vol. 45, pp. 107–118.
1971c. The identities and allocations of *Taeromys paraxanthus* and *T. tatei*, two taxa based on composite holotypes (Rodentia, Muridae). *Ibid.*, vol. 45, pp. 127–138.
1971d. The taxonomic status of *Rattus tondanus* Sody and notes on the holotypes of *R. beccarii* (Jentink) and *R. thysanurus* Sody (Rodentia, Muridae). *Ibid.*, vol. 45, pp. 147–157.
1971e. The taxonomic status of *Rattus dammermani* Thomas and *Rattus toxi* Sody (Rodentia, Muridae), of Celebes. Beaufortia, vol. 18, pp. 205–216, figs. 1, 2.

OW-YANG, C. K.
1971. Studies on the nematode parasites of Malaysian rodents. 1. The Rhabdiasidea, Trichuridea and Oxyuridea. Jour. Helminth., vol. 55, pp. 93–109, 1 map.

ROBINSON, H. C., AND C. B. KLOSS
1916. Preliminary diagnoses of some new species and subspecies of mammals

and birds obtained in Korinchi, West Sumatra, Feb.-June, 1914. Jour. Straits Branch Roy. Asiatic Soc., no. 73, pp. 269–278.

1919. On a collection of mammals from the Bencoolen and Palambang Residencies, South West Sumatra. Jour. Fed. Malay States Mus., vol. 7, pp. 257–291, 1 fig.

SCHWARZ, E.

1961. The taxonomic position of *Rattus pesticulus* Thomas 1921. Ann. Mag. Nat. Hist., ser. 13, vol. 4, p. 415.

SCHWARZ, E., AND H. K. SCHWARZ

1967. A monograph of the *Rattus rattus* group. Ann. Esc. Nac. Cien. Biol., Mexico, vol. 14, pp. 79–178.

SODY, H. J. V.

1930. Overzicht van de ratten van Java met beschrijving van een nieuwe subspecies. Zool. Meded. Rijksmus. Natuur. Hist., Leiden, vol. 13, pp. 100–140.

1933. Ten new mammals from the Dutch East Indies. Ann. Mag. Nat. Hist., ser. 10, vol. 12, pp. 430–442.

1941. On a collection of rats from the Indo-Malayan and Indo-Australian regions (with descriptions of 43 new genera, species, and subspecies). Treubia, vol. 18, pp. 255–325.

TATE, G. H. H.

1936. Results of the Archbold Expeditions. No. 13. Some Muridae of the Indo-Australian region. Bull. Amer. Mus. Nat. Hist., vol. 72, pp. 501–728, figs. 1–32.

1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Ibid.*, vol. 97, pp. 187–430, figs. 1–4.

THOMAS, O.

1920. On mammals from Ceram. Ann. Mag. Nat. Hist., ser. 9, vol. 6, pp. 422–431.

1921. On a new genus and species of shrew, and some new Muridae from the East-Indian Archipelago. *Ibid.*, ser. 9, vol. 7, pp. 243, 249.

VAN HEURN, W. C.

1931. Sawah-ratten-bestrijding in bergterrein (with a summary in English). Instituut voor Plantenziekten van het Algemeen Proefstation voor den Landbouw, Bull. no. 23, pp. 1–48, pls. 1–9.

VAN PEENEN, P. F. D., P. F. RYAN, AND R. H. LIGHT

1969. Preliminary identification manual for mammals of South Vietnam. United States National Museum, Smithsonian Institution, Washington, D.C., pp. i–vi, 1–310, figs. 1–81.

VAN STEENIS, C. G. G. J.

1958. Vegetation map of Malaysia (1: 5,000,000). Unesco Humid Tropics Research Project.

WALLACE, A. R.

1872. The Malay Archipelago: the land of the orang-utan and the bird of paradise. A narrative of travel, with studies of man and nature. Fourth edition. London, Macmillan and Co., pp. i–xvi, 1–653, figs. 1–51, maps 1–10.

WOOD, B. J.

1969. The extent of vertebrate attacks on the oil palm in Malaysia. 2nd. Malaysian Oil Palm Conference, 1968. Progress in oil palms, pp. 162–184.

1971a. Investigations of rats in ricefields demonstrating an effective control method giving substantial yield increase. PANS, vol. 17, no. 2, pp. 180–193, figs. 1–5.

1971b. Sources of reinfestation of oil palms by the wood rat (*Rattus tiomanicus*). *In* Wastie, R. L., and B. J. Wood (eds.), Crop protection in Malaysia, 1970. Incorporated Society of Planters, Kuala Lumpur, pp. 146–165, figs. 1–5.

YONG, H. S.

1969. Karyotypes of Malayan rats (Rodentia-Muridae, Genus *Rattus* Fischer). Chromosoma, vol. 27, pp. 245–267, figs. 1–14.

YOSIDA, T. H., K. TSUCHIYA, AND K. MORIWAKI

1971. Karyotypic differences of black rats, *Rattus rattus*, collected in various localities of East and Southeast Asia and Oceania. Chromosoma, vol. 33, no. 3, pp. 252–267, figs. 1–4.